CESTODES IN MAMMALS : THE ZOOGEOGRAPHY OF SOME PARASITE-HOST ASSEMBLAGES

BY

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" Manche Thiere haben, ihnen ganz eigene, Eingeweidewürmer, die in anderen Thieren nicht gefunden werden. "
Johann Gottfried Bremser, 1819.

The Recent mammalian fauna of the region around Bering Strait (between ca. long. 150° E, in Eurasia, and long. 140° W, in North America) comprises more than 70 species, representing approximately 40 genera. These species can be arranged in five categories on the basis of their origins and distribution (Table 1) (cf. Rausch, 1977). The cestodes in most of these mammals are relatively well known, but further taxonomic revisions will be required to establish the identities and distributional status of species in shrews (Soricidae) and in some rodents of the family Arvicolidae.

TABLE 1. — Composition of the Recent terrestrial mammalian fauna around Bering Strait (between ca. long. 150° E and long. 140° W).

I. Circumpolar, associated with coastal tundra and/or sea-ice (2 species).
- *Alopex lagopus*
- *Ursus maritimus*

II. Holarctic (15 species).
- *Sorex arcticus*
- *S. cinereus*
- *Citellus parryi*
- *Clethrionomys rutilus*
- *Microtus oeconomus*
- *Lemmus sibiricus*
- *Canis lupus*
- *Vulpes vulpes*
- *Ursus arctos*
- *Mustela erminea*
- *Mustela nivalis*
- *Gulo gulo*
- *Felis lynx*
- *Rangifer tarandus*
- *Alces alces*

III. Beringian endemics (4 species).
West (Eurasia)
- *Marmota camtschatica*

East (North America)
- *Marmota broweri*
- *Microtus abbreviatus* (including *M. miurus*)
- *Lepus othus*

IV. Palaearctic species *
Chukotsk Peninsula (24 species)
- *Sorex* (6)
- *Neomys* (1)
- *Eptesicus* (1)
- *Myotis* (1)
- *Lepus* (1)
- *Ochotona* (1)
- *Pteromys* (1)
- *Sciurus* (1)
- *Tamias* (1)
- *Marmota* (1)

Apodemus (1)
Myopus (1)
Alticola (1)
Microtus (2)
Clethrionomys (1)
Martes (1)
Lutra (1)
Ovis (1)

V. Nearctic species *

Alaska (31 species)
Sorex (2)
Microsorex (1)
Myotis (1)
Lepus (2)
Ochotona (1)
Glaucomys (1)
Tamiasciurus (1)
Tamias (1)
Marmota (3)
Peromyscus (1)
Zapus (1)
Castor (1)
Synaptomys (1)
Ondatra (1)
Microtus (4)
Erethizon (1)
Canis (1)
Ursus (1)
Mustela (1)
Martes (1)
Lutra (1)
Oreamnos (1)
Ovibos (1)
Ovis (1)

TOTAL : 72 species.

Two species, the polar bear, *Ursus maritimus* Phipps, and the arctic fox, *Alopex lagopus* L., have a circumpolar distribution. No host-specific helminths are known from the polar bear.

Cestodes of three species, *Taenia crassiceps* Zeder, 1800, *T. polyacantha* Leuckart, 1856, and *Echinococcus multilocularis* Leuckart, 1863, characteristically occur in the arctic fox throughout most of its geographic range (not including Greenland and some arctic islands where intermediate hosts are absent). These cestodes, not strictly host-specific, occur also in foxes of the genus *Vulpes*. They seem clearly to be of palaearctic origin, having extensive geographic ranges in Eurasia.

In North America, *T. crassiceps* occurs throughout the zone of tundra, but it is present also in red foxes, *Vulpes vulpes* L., at lower latitudes in the eastern part of the continent. However, because of early introductions of red foxes from Europe, the cestode might also have been introduced. *T. polyacantha* is known only from the zone of tundra. Such was the case also with *E. multilocularis*, but this cestode has become established only recently in central North America, apparently having been dispersed by arctic foxes emigrating southward from the zone of tundra bordering the western shore of Hudson Bay (Rausch, 1981).

The arctic fox is of palaearctic origin, and probably spread into Beringia during the late Pleistocene. The geographic ranges of *T. polyacantha* and *E. multilocularis* are compatible with this concept.

Comparatively few host-specific cestodes are known from holarctic species of mammals, but these few are of particular zoogeographic interest.

The assemblage comprised of the arctic ground squirrel, *Citellus parryi* (Richardson), an anoplocephalid cestode, *Anoplocephaloides transversaria* (Krabbe, 1879), and presumably, an oribatid mite as intermediate host exhibits some unusual features, which can be discussed only with reference to cestodes in marmots, *Marmota* spp.

As has been reported by Rausch and Rausch (1971), marmots in Eurasia and North America have distinct cestode-faunas, involving species of the families Anoplocephalidae and Catenotaeniidae. In Eurasian marmots, from Middle Asia to the west, occur *Anoplocephaloides transversaria*, *A. ryjikovi* (Spasskii, 1950), and *Ctenotaenia marmotae* (Frölich, 1802) ; in North America, *Diandrya composita* Darrah, 1930 and *Catenotaenia reggiae* Rausch, 1951. The genus *Marmota* is of nearctic origin, with a stratigraphic range in Eurasia extending back to the Villafranchian. It is thus evident that the two cestode-faunas were acquired independently by the two groups of marmots since their separation in the early Pleistocene. With the exception of *A. transversaria*, these cestodes have been recorded only from members of the genus *Marmota*.

* Number of species follows name of genus. List includes Beringian endemics (III, above) but does not include the still undetermined number of species of varying lemmings (genus *Dicrostonyx*).

In the course of dispersal of *Marmota* westward across Beringia, it appears that a population was left in the Beringian region, and that this early-Pleistocene form was the precursor of two Recent species, *M. camtschatica* (Pallas) and *M. broweri* Hall and Gilmore, which respectively inhabit the mountains of northeastern Siberia and the Brooks Range in northern Alaska. The apparent absence of any cestodes in *M. camtschatica* (see Kapitonov, 1963 ; Ryzhikov *et al.*, 1978) indicates that the Beringian population of marmots became disjunct before any cestodes were acquired, and that there was no subsequent contact with marmots in Middle Asia through which transfer of cestodes could occur. The presence of the two nearctic species of cestodes in *M. broweri* can be attributed to transfer following secondary contact with the nearctic *Marmota caligata* (Eschscholtz), which extended its range northward into northwestern North America during post-glacial time. A second species of nearctic marmot, *M. monax* L., also spread into what is now Alaska during post-glacial time, but there are no records of cestodes from it.

The presence of *A. transversaria* in the Amphiberingian ground squirrel, *C. parryi*, has been recognized only recently, following the collection of material on the Chukotsk Peninsula. Comparisons with the type of *A. transversaria* and with *A. wigginsi* (Rausch, 1954), described from *C. parryi* in arctic Alaska, disclosed that only a single species was represented. However, the nearctic form differed in arrangement of the genital pores, which were irregularly alternating, rather than unilateral as in the Eurasian specimens. This appears to represent the first reported example of allopatric morphologic divergence at the infraspecific level in a cestode in a single species of host. As it may be assumed that the distribution of *C. parryi* in Beringia was continuous during the last glacial period, it follows that this divergence has occurred since rising sea-level separated the Eurasian and North American populations, approximately 12,000 years ago.

The cestode fauna of rodents in the family Arvicolidae is composed of numerous species representing mainly the families Hymenolepididae and Anoplocephalidae. The distributional status of some species in the genera *Hymenolepis* Weinland, 1858 *sensu lato*, *Andrya* Railliet, 1893, and *Anoplocephaloides* Baer, 1923 is still uncertain, pending further taxonomic revision. Consequently, the number of holarctic species has not been determined. In general, host-specificity is not strongly expressed in cestodes occurring in these rodents.

One of the holarctic species in voles of the genus *Microtus* is *Paranoplocephala omphalodes* (Hermann, 1783), which has an extensive geographic distribution in the Palaearctic. In North America, this cestode has been recorded only from the northern vole, *Microtus oeconomus* (Pallas), which also has an extensive range in the Palaearctic, and from the nearctic representative of the subgenus *Stenocranius*, *M. abbreviatus* Miller (including *M. miurus* Osgood). *M. abbreviatus* is a Beringian endemic, whose present range hardly exceeds the geographic limits of the former Beringian Refugium. The distribution of *M. oeconomus* in North America indicates that it was a late Pleistocene immigrant to Beringia, from which it dispersed eastward during post-glacial time. *P. omphalodes* apparently spread into Beringia with the northern vole, and was transferred to the indigenous *M. abbreviatus*.

The brown lemming, *Lemmus sibiricus* (Kerr), is a holarctic species whose presence in Beringia dates from the Villafranchian at Cape Deceit. Rausch and Rausch (1975) considered that the distribution of the brown lemming would have been continuous in the arctic lowlands of northeastern Siberia and Beringia during glacial periods. This concept is supported by the widespread occurrence of a host-specific cestode, *Anoplocephaloides lemmi* (Rausch, 1952), which has been recorded in Iakutia (Gubanov and Fedorov, 1970), Chukotka (Rausch and Smirnova, unpublished), Alaska (Rausch, 1952), and on the western coast of Hudson Bay, at Rankin Inlet (Rausch, unpublished).

Some cestodes in carnivores of the family Mustelidae are of interest, relative to the zoogeography of parasite-host assemblages. *Taenia martis americana* Wahl, 1967 occurs in martens, *Martes* spp., in eastern Eurasia and in North America, whereas *T. m. martis* (Zeder, 1803) is a parasite of mustelids in western Eurasia. The holarctic distribution of the former supports the concept, based on morphologic and other criteria, that the palaearctic *Martes zibellina* L. and the nearctic *M. americana* (Turton) are closely related or, perhaps, conspecific. The fossil record indicates that *Martes* invaded North America from the Palaearctic during early Würm time.

Taenia twitchelli Schwartz, 1924 is a host-specific cestode in the wolverine, *Gulo gulo* L., in the

Nearctic. The parasite-host assemblage, additionally involving rodents, typically *Marmota* spp., as intermediate host seems to have arisen following the dispersal of wolverines into Beringia during the late Pleistocene. Morphologically, *T. twitchelli* most closely resembles *T. martis*, from which it may be derived. Thus far, there are no published records of cestodes in the wolverine in Eurasia.

Cestodes of zoogeographic interest occur in various of the nearctic species of mammals. The present discussion is limited to those occurring in pikas, *Ochotona* spp., and in sheep, *Ovis* spp., which appear to have had similar distributional histories.

According to Thenius (1972), the leporid and ochotonid lines diverged during the Eocene, and the earliest definitely recognizable ochotonids are known from the Oligocene of Eurasia. Thereafter, radiation led to dispersal to Africa and to North America (Miocene). The family is represented by a single Recent genus, *Ochotona*, of which all but two species are palaearctic. The two species in western North America are derived from a late Pleistocene precursor which spread from Beringia. The affinities of the nearctic species would appear to be with *O. hyperborea* (Pallas), which occurs widely in northeastern Siberia as well as on the islands of Hokkaido and Sakhalin. However, karyologic studies have shown that the latter has a diploid number of only 40, whereas that of the nearctic species, *O. princeps* (Richardson) and *O. collaris* (Nelson), is 68. The nearctic species have the same diploid number as the palaearctic *O. pusilla* (Pallas), which Vorontsov and Ivanitskaia (1973) considered to have the most primitive karyotype of any species thus far investigated. Consequently, *O. hyperborea* may represent a late Pleistocene migrant from the south.

Pikas would seem to have had an extensive geographic distribution in western North America during the last interglacial, after which disruption of their range by the last (Würm) glaciation left populations in Beringia and to the south of the continental ice. The populations diverged, as indicated by differences in karyotypes (Rausch and Ritter, 1973), and have remained widely disjunct.

The pikas have distinctive helminth faunas, indicative of a long process of coevolution in Eurasia. Their cestodes represent three genera, of which two, *Diuterotaenia* Gvozdev, 1961 and *Ectopocephalium* Rausch and Ohbayashi, 1974, are monotypic, known respectively from Siberia and Nepal. The genus *Schizorchis* Hanson, 1948 is polytypic, represented by two species in North America and an undetermined number in Eurasia. It was considered earlier that the presence of *S. ochotonae* Hanson, 1948 and *S. caballeroi* Rausch, 1960 in *Ochotona princeps* and *O. collaris*, respectively, was indicative of divergence paralleling that in their hosts. However, the recent identification of *S. caballeroi* from the southern *O. princeps* indicates that the relationships involved are more complex. Morphologically, *S. caballeroi* more closely resembles the cestodes, tentatively designated *S. altaica* Gvozdev, 1951, in *O. hyperborea* in Chukotka. A distinctive species, *S. yamashitai* Rausch, 1963, occurs in *O. hyperborea* on the island of Hokkaido, to which it spread in the late Pleistocene (Kotani, 1969). Additional collections of cestodes from pikas will be required to establish the identity and distribution of *Schizorchis* spp. in Eurasia.

The two nearctic species of sheep, *Ovis dalli* Nelson, in the Beringian region, and *O. canadensis* Shaw, in southwestern North America, appear to have had a distributional history similar to that of the pikas. As determined by Vorontsov *et al.* (1972) and Korobitsyna *et al.* (1974), the Amphiberingian precursor of the two nearctic species and of *O. nivicola* Eschscholtz in northeastern Siberia probably had a diploid number of 54 chromosomes. Segregation of the western and eastern populations might have occurred as late as the penultimate glacial period, after which the latter dispersed southward from Beringia, probably forming a continuous population in western North America during the last interglacial. As in the case of *Ochotona*, disjunct northern (Beringian) and southern populations were segregated by the subsequent glaciation. Divergence led to the differentiation of the three Recent species. The two in North America retained the ancestral number of 54 chromosomes, whereas the number in *O. nivicola* was reduced to 52 by a centric fusion (Voronstov and Liapunova, 1973).

A host-specific cestode, *Wyominia tetoni* Scott, 1941, was described from *Ovis canadensis* and later (1961) recorded from *Ovis dalli* in the Wrangell Mountains of Alaska (Rausch, unpublished). Since *W. tetoni* is not known from *Ovis* spp. in Eurasia, formation of the parasite-host assemblage must have occurred following the segregation of western and eastern populations in Beringia, but

before the subdivision of the latter by the last (Würm) glaciation. These findings support the concept that the two nearctic species of sheep are derived from a common, late Pleistocene precursor.

From the limited data now available, it is evident that some parasite-host assemblages as here conceived can be traced back at least to the penultimate glacial period. Divergence in cestodes of a given genus may or may not parallel genetic and/or phenotypic divergence in the host, as demonstrated by the greater age of the species of cestode in some assemblages. This indicates that speciation in the mammalian host does not in itself necessarily involve selection pressures that would affect the fundamental relationship of the component organisms. Although maximal ages can be established for some assemblages, minimal ages can be deduced only within broad limits.

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DISCUSSION

ANDERSON. — Have you any idea of the origin of species of tapeworms in *Ovis* in North America ?

RAUSCH. — *Wyominia* does not have morphologic features by which its derivation can de determined.

ANDERSON. — Can you say any thing about the possible role of pleistocene extinction ?

RAUSCH. — It is obvious that helminths become extinct if their host species become extinct. Helminths with a relatively wide host range would stand a better chance of surviving in a period such as the Pleistocene faunal disruptions. An example for North America would be *Equus* spp. and their parasites which disappeared in North America but survived in The Old World.

SCHAD. — Is anything known about the pinworms (*Skrjabinema*) of *Ovis dalli* and *Ovis nivicola* ?

RAUSCH. — No.

SCHAD. — They should prove interesting. *Skrjabinema* occurs in *Ovis canadensis*.

SPRENT. — You mentioned in your paper that *T. solium* and *T. saginata* can only have been human parasites fro 16.000 years. Do you think this time span is long enough for the establishment of such a high degree of specificity together with the actual morphologic differentiation of the scolex in *T. saginata* ?

CHABAUD. — Certains parasites semblent capables d'une évolution très rapide. Par exemple, un Digène apparemment endémique chez un bovidé domestique malgache. L'exemple le plus étonnant que je connaisse est celui d'*Heligmosomoides polygyrus* étudié par Marie-Claude Desset.

C'est un parasite du Mulot ou de la Souris domestique d'Europe occidentale. Il effectue une spéciation bien perceptible morphologiquement chez la souris domestique des États-Unis, puis une seconde spéciation chez certains Cricétidés nord-américains. Donc 2 spéciations successives en 300 ans.

BEVERIDGE. — Do you have any comments to make on the morphology of *Anoplocephaloides* species on either side of the Bering Strait ? The reason for the question is that *Ctenotaenia marmotae* from the European marmot seems to have risen from species of *Anoplocephaloides* peculiar to this host. In contrast, in America, *Pseudacittotaenia* seems to have arisen from North American species of *Anoplocephaloides* from American hosts.

RAUSCH. — Two species of *Anoplocephaloides* are holarctic : *A. transversaria* in Marmota, and *A. lemmi* in *Lemmus*. Infraspecific variation has been mentioned. There appears to be one other holarctic species in *Microtus*, but its status has not been resolved. I do not recognize any particular morphologic pattern with respect to these Cestodes east and west of Bering Strait.

PETTER F. — Avez-vous des informations concernant les rapports des lièvres arctiques avec *Lepus timidus* ?

RAUSCH. — The three species, *Lepus timidus*, *L. othus* and *L. arcticus*, are very similar. From cranial characters, multivariate analysis has shown that they lall into discrete groups. Their chromosomes have not yet been adequately compared.

BEVERIDGE. — Regarding species of *Lepus*, one cestode *Mosgovojia pectinata* is remarkably uniform from *Lepus* spp. in Africa, Europe, Asia, and Alaska. It gives no real information on the *Lepus* spp. on either side of the Bering Strait, but different forms of the species do exist in *Sylvilagus* and in the more southern American species of *Lepus* e.g. *L. townsendi*.

HUGOT. — Les oxyures de Leporidés appartenant au genre *Passalurus* comprennent deux espèces. La plus primitive, *P. nonanulatus*, est la plus largement répandue, puisqu'on la rencontre de l'Amérique du Sud à l'Afrique du Sud, en passant par l'Asie et l'Europe ; dans le nouveau monde chez *Lepus americanus*, *Sylvilagus floridanus* et *Romerolagus diazi* ; dans l'ancien monde chez *Lepus sinensis*, *Lepus granatensis* et *Pronolagus crassicaudatus*. La seconde espèce, *P. ambiguus*, plus évoluée, semble être limitée à l'aire de répartition d'*Oryctolagus cuniculus* et de *Lepus capensis* (= *europeus* d'après F. Petter). Cette dernière espèce n'a été signalée qu'une seule fois chez un autre hôte, en Amérique du Nord, et il semble qu'il s'agisse soit d'une erreur, soit de la capture par un hôte autochtone d'un parasite introduit par le lièvre européen qui a été acclimaté dans la même région.